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ON THE DIET AND FEEDING BEHAVIOR OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX* (GIRARD)*

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INTRODUCTION

Plankton has long been known to constitute the main food of such commercially important pelagic fishes as herring and sardines. However, existing literature on this subject, in regard to fish preference either for zooplankton or phytoplankton, quite often presents contradictory conclusions by different authors. Sometimes this is true for one and the same species from the same area and period, and even when investigation is based on the same material collected, as was the case of the Lewis-Parr controversy. It was especially difficult to ascertain whether there was a definite preference for zooplankton over phytoplankton, or vice versa, in the diet of the species investigated. For example, food habits of the Pacific sardine, *Sardinops caerulea*, have been investigated by several researchers, of whom Lewis (1929) was the first. On the basis of 207 stomachs, he concluded that this fish is primarily a phytoplankton feeder. Parr (1930), using Lewis' own data, reversed his conclusion by recognizing the zooplankters found in the stomach contents as "the only real objects of special pursuit." Presence of phytoplankton in the contents, he explained, was "merely due to incidental ingestion with other elements of the diet."

Hart and Wailes (1932) examined 285 sardine stomachs from the waters of British Columbia. They found 2 dominant types of food: Diatomaceae and Crustacea, thus indicating the sardine to be omnivorous in its food habits. Radovich (1952), on the basis of 42 sardine stomachs from Baja California and

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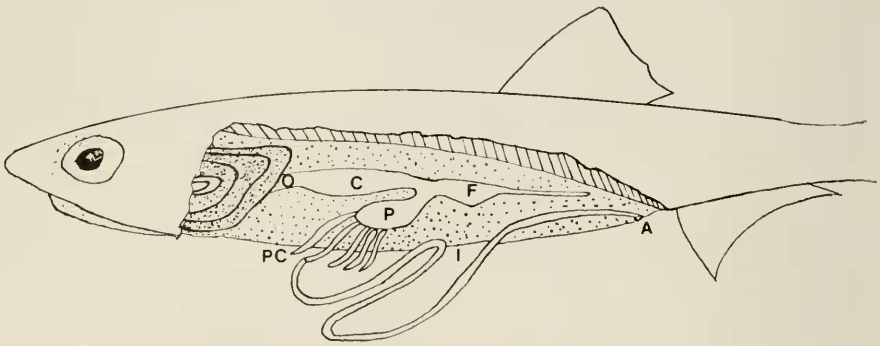

Figure 1. Diagrammatic representation of the alimentary tract of the northern anchovy. O.—Oesophagus, C—Cardiac stomach, P—Pyloric stomach, F—Fundus of stomach, I—Intestine, PC—Pyloric caeca, A—Anus.

southern California, regarded this fish as a carnivorous animal living mostly on zooplankters (chiefly copepods).

An anonymous author (1952), after examination of 273 stomachs, agreed in part with Radovich's conclusion by saying that the chief food of sardine larvae is "very early stages of small copepods." In stomachs of the adult sardines, zooplankton was found in 100 percent and phytoplankton in only 75 percent.

Hand and Berner (1959) examined 571 sardines, reporting that crustaceans are the "major food" (copepods being the most important item) which, on the average, contributed 89 percent of the organic matter, while phytoplankton contributed only 11 percent. This proportion of food types in the stomach contents showed a high correlation with plankton samples taken at the same place and time.

Regardless of demonstrated preference in favor of zooplankters in the preceding 2 cases, the sardine exhibited a dual mode of feeding, consuming both zoo- and phytoplankton, and therefore should be considered omnivorous in its food habits.

The same contradictory conclusions were made by the investigators who studied food habits of the Japanese sardine—the iwashi, *Sardinops melanosticta*. Kishinouye (1907) concluded that the juvenile fish appeared to be carnivorous in food habits, being dependent on zooplanktonic food, and that the adult fish becomes vegetarian, feeding on phytoplankton.

Deriugin (1933) assumed that the iwashi eats both types of plankton without specific discrimination, according to which is present in the water mass of a given season. In other words, he identified the iwashi as an omnivorous animal. Gaĭl (1934) at first was of the opinion that the phytoplankters were the only basic food of the sardine in the northwestern parts of the Sea of Japan. He admitted that sardine stomachs sometimes were found filled with copepods, but

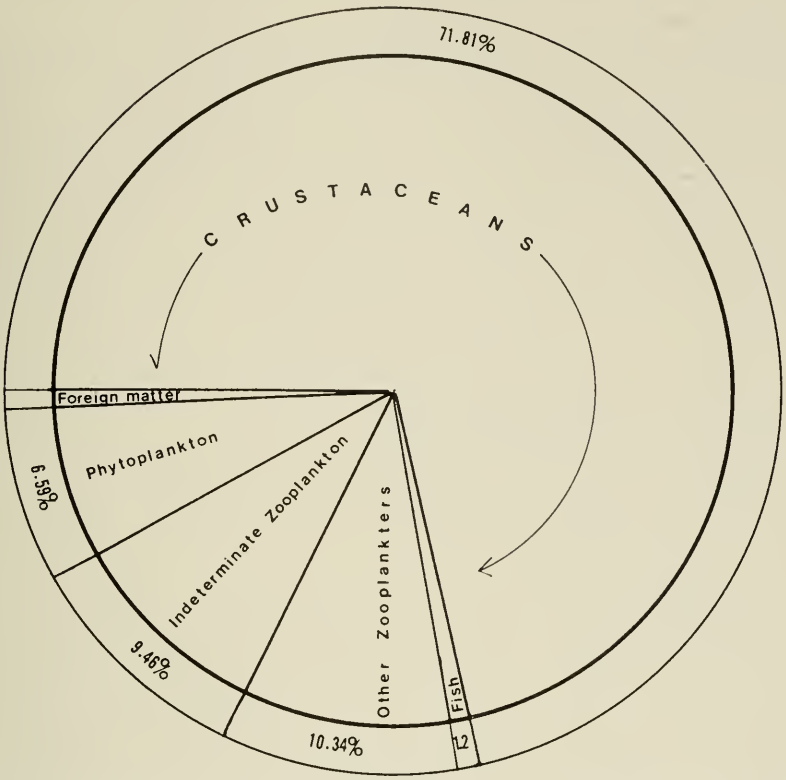

Figure 2. Percentage distribution of dominating food items in 667 anchovy stomachs.

said that this "in no measure would diminish the role of phytoplankton as the basic food of iwashi." Two years later (1936), apparently after examination of a greater number of stomachs, he came to regard the zooplankton (copepods) as the preferred food of the Japanese sardine. Koganovskaia (1934) recorded dominance of one or the other type of plankton in the sardine stomachs by season (zooplankton in May, June, and October, and phytoplankton in August and November) in direct relation to the presence of these food types in the associated plankton samples. Koganovskiĭ (1935) concluded that the iwashi is not selective in its food habits. "It feeds on phyto- and zooplankton with mass predominance of either [in their stomachs] in direct dependence on their predominance in the surrounding water. In cases where fish descended to near-bottom layers in shallows, benthic crustaceans and even detritus were found in the fish stomachs." Brodskiĭ and Iankovskaia (1935) reported predominance of zooplankters (chiefly copepods and protozoans) in 110 stomachs examined. The number of distended stomachs filled with the crustaceans bore direct relation to the amount of zooplankton in the sea-masses and of copepods in the plankton hauls. With phy-

toplankton they observed a nonconformity between the quantities in the plankton samples and the stomachs. These authors assumed that the role of phytoplankton in the diet of the Japanese sardine "can be fairly large in general (although second to copepods), but is reduced to the role of the so-called 'forced diet' in the absence of concentrations of zooplankton." Brodskiĭ (1936) speaking of the food of the iwashi in Possiet Bay, mentioned that it included almost all the microplankton of the area investigated, but that stomachs "filled to capacity were noted only in the presence of Copepoda." Predominance of copepods over the other food items was at times exceptionally high, reaching 95–100 percent. Iankovskaia (1937) confirmed the outstanding role of zooplankters, chiefly copepods, in the sardine diet in conformity with the abundance of them in the sea; in almost every case, greater abundance of plant organisms in the sea coincided with low filling of the stomachs.

The above investigations clearly indicated a dual mode of feeding in the Japanese sardine, with, however, preference for the animal food.

The Indian sardines *Sardinella gibbosa* and *S. longiceps* are regarded as carnivorous animals feeding on zooplankton, chiefly on copepods (Madras Fisheries Department, 1933, 1936).

According to Davies (1957), the South African pilchard, *Sardinops ocellata*, consumes phytoplankton "to far greater extent than the zooplankton during the greater part of the year." The year's mean ratio was found to be 2:1. He examined 16,664 stomachs during 1953–56, and concluded the South African sardine to be a vegetarian which also feeds on zooplankton "at times when abundance of phytoplankton has become diminished." In reference to zooplankton Davies stated that "the most important group in the zooplankton eaten by pilchards is the copepoda: copepods were eaten throughout the year but occurred in stomach contents in largest numbers in summer and in winter." In the opinion of the present writer, if plant food is equal to 67 percent of the total, and animal food estimated at 33 percent, the South African sardine falls in the category of an omnivorous animal, regardless of a statistical "preference" for phytoplankton.

Regarding the feeding habits of the (Atlantic) European sardine, *Sardina pilchardus*, we refer to the investigations conducted by Hickling (1945) who examined 2,400 stomachs of pilchard taken off the coast of Cornwall in 1935–38. He established that these fish feed seasonally on either of the two types of plankton. Among the most important and consistently recurring organisms, Hickling listed (in order of importance) copepods, euphausiids, mysids, amphipods, and many other larval and young crustaceans. Next in importance were found to be diatoms and peridinians. Once again we can see a dual mode in food habits, thus letting us classify Cornish pilchard as an omnivorous animal displaying preference toward animal food.

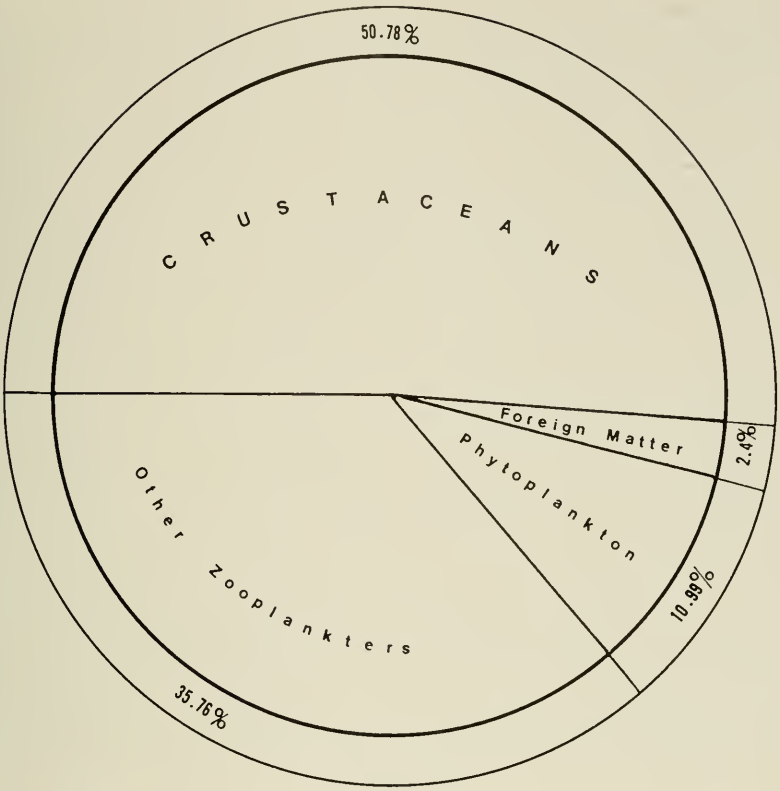

Figure 3. Percentage frequency of food type incidence in 840 filled stomachs of the anchovy.

With such a confusing picture of the food habits of the ecologically related pelagic species in mind, the present studies on feeding behavior of the Northern Anchovy, *Engraulis mordax*, were initiated in 1965 and concluded in 1968. It was intended to find out, as accurately as possible with the opportunities available, the actual diet of our anchovy, its mode of feeding, and its ability to discriminate food types. Material presented on the following pages is based on the collections of stomachs, on visual observations in aquaria and in the ocean, and on review of the available, though scant, literature.

MATERIAL

Three basic collections of anchovy stomachs were made by the writer, and 3 supplementary ones were provided by other collectors. The first collection was made in Monterey Bay, central California, in May 1965, through assistance of Mr. Tom Arcolea, a live-bait fisherman in Monterey. One hundred and thirty-

nine live anchovies, ranging in size from 87 mm. to 215 mm. standard length, were randomly picked out of his night catches in lampara nets. The second basic collection was made during the survey cruise of M/V *Alaska* of the Department of Fish and Game on September 15—October 3, 1965 in northern Baja California, Mexico, between Acme Rock and the California-Mexico border. Electric light and blanket net, and midwater trawl were used as collecting gear. Four hundred and nine anchovies, ranging in size from 43 mm. to 149 mm. standard length, were obtained and their stomachs preserved for analysis. The third basic collection was made in 1966 during the October survey cruise of the same research vessel from Geronimo Island in northern Baja California to Point Conception in southern California, when 220 stomachs were obtained from anchovies ranging from 50 mm. to 155 mm. standard length which were collected using chiefly the midwater trawl.

In addition to these basic collections, 3 small supplementary ones were made by other persons. Dr. Reuben Lasker contributed 2 sets of stomach contents from northern Baja California, one consisting of 20 specimens from fish 121 mm. to 138 mm. standard length collected at Bahia Soledad in the month of June, 1965, and the other one numbering 40 specimens from Ensenada Fisheries, collected in October of the same year (no information on the size of the fish was provided). The third supplement came from southern California waters. It consisted of 98 frozen anchovies, 60 mm. to 134 mm. standard length, collected and preserved by Mr. Deon L. Hamilton while aboard M/V *Alaska*, surveying fish populations in January–February, 1968, mostly in Santa Monica Bay.

METHODS

Fishing gear used during this study consisted of midwater trawl, lampara net, blanket net, electric light and blanket net (at night)[1], dip net, and hook-and-line (treble) for snagging fish. The trawl was used most generally. The other types of fishing gear mentioned were used occasionally. Immediately after the fish were caught, 10 to 25 specimens were randomly picked out. Their stomachs (cardiac, pyloric, and fundus) including esophagus were removed, (fig. 1), freed from fat, slightly rinsed in cold salt water, and preserved in 4 percent formalin. All stomachs of a given sample were kept in a jar bearing necessary information on the label inserted in, or attached to, the jar. No concurrent plankton sampling was done. In the laboratory, the contents of each stomach were removed and placed in individual vials for macroscopic and microscopic examination. All items of the contents of individual stomachs were identified in as great detail as practicable, their relative proportions determined by wet volume, and recorded under 3 categories: dominating, second in order, and insignificant. Then all individual records were grouped in a sample table to

[1] The blanket net and its use in sampling populations of commercially important pelagic fishes was described in detail by Radovich and Gibbs (1954).

show the frequency of occurrence within the sample, and finally all samples of a given collection were tabulated in 6 tables (nos. 2 through 7). Evaluation of preferential tendencies of the anchovy in its diet was based on those stomach contents in which predominance of a certain food type over the others was clearly evident.

RESULTS

Altogether, contents of 926 stomachs were examined and, in accordance with the amount of food found, were classified as empty, very poor, poor, filled to full capacity, ¾ capacity, ½ capacity, and ¼ capacity. The majority of the stomachs fell into categories "poor" (299) and "very poor" (218) and 86 stomachs were empty (table 1).

The best filled stomachs were found in fishes caught during the day or in fishes caught at night attracted by an electric light under which they were feeding on plankton swarming within the illuminated zone. Less filled stomachs and most of the empty ones were found in fishes caught in the midwater trawl during night sampling. Baxter (1967) also recognized anchovies "chiefly" as daytime feeders. A dominance of one type of food over the others (by wet volume) was recorded in 667 stomachs (tables 1 and 8). In a spring collection from Monterey Bay (May 1965), dominance was recorded in 81 out of 139 stomachs. The zooplanktonic forms (64.2 percent) definitely exceeded the phytoplanktonic organisms (35.8 percent) (table 2). In the fall collection from northern Baja California (September 1965) of 409 stomachs, dominance was recorded in 283 in favor of zooplankters (98.5 percent), and foreign matter (1.41 percent). On no occasion were the phytoplankters found in significant volume (table 3). In the autumn collection from southern California made in October of 1966, dominance was recorded in 165 out of 220 stomachs. This dominance was exclusively in favor of zooplankters. The phytoplanktonic organisms on only one occasion occupied second place (table 4). In supplementary collections, dominance of certain food types was recorded as follows: in the June collection of 20 stomachs (1965) from northern Baja California dominance was recorded in 18, with precedence of the phytoplankters (83.33 percent) over the zooplanktonic organisms (16.67 percent) as shown in table 5. In the fall collection of 40 stomachs from the same area, dominance was evident in 23 stomachs in favor of zooplankters alone (table 6). In the winter collection from southern California (January–February 1968) dominance was displayed in 97 out of 98 stomachs in favor of zooplanktonic forms alone; however, in 33 cases the phytoplankton occupied second place (by wet volume) (table 7).

In 667 cases of recorded dominance of zooplankters the top priority belongs to crustaceans (71.81 percent), the second place being taken by other zooplankters (11.54 percent), and the third place by indeterminate zooplanktonic remains and fleshy parts (9.46 percent). The fourth in subordinate order was phyto-

TABLE 1. *Stomachs of northern anchovy by localities of collection and food content as related to stomach capacity.*

Collection	*Number of Samples*	*Number and Percentages* — *Stomach filling (wet volume)* — *Full*	¾	½	¼	*Poor*	*Very Poor*	*Empty*	*Total*	*Dominating*[4]
No. 1–Central California, May 1965	9	16[1]	2	17	—	5	73	26	139	(81)
		11.53%	1.44%	12.23%	—	3.59%	52.51%	18.70%	100%	(58.27%)
No. 2–N. Baja California, September 1965	29	26[2]	33	40	26	127	122	35	409	(283)
		6.36%	8.07%	9.77%	6.36%	31.05%	29.83%	8.56%	100%	(69.19%)
No. 3–N. Baja California and southern California, October 1966	21	18[3]	24	37	44	53	21	23	220	(165)
		8.18%	10.91%	16.82%	20.0%	24.09%	9.55%	10.45%	100%	(75.0%)
No. 4–N. Baja California June 1965	1	6	4	7	—	2	—	1	20	(18)
		30.0%	20.0%	35.0%	—	10.0%	—	5.0%	100%	(90.0%)
No. 5–N. Baja California October 1965	2	1	—	19	—	18	2	—	40	(23)
		2.5%	—	45.5%	—	45.0%	5.0%	—	100%	(57.50%)
No. 6–Southern California January–February 1968	7	—	—	3	—	94	—	1	98	(97)
		—	—	3.06%	—	95.92%	—	1.02%	100%	(98.98%)
Total	69	67	63	123	70	299	218	86	926	(667)
		7.24%	6.80%	13.28%	7.56%	32.29%	23.54%	9.29%	100%	(72.03%)

[1] Out of 16, 2 stomachs were "gorged" to the point of bursting on cutting the abdomen.
[2] Out of 26, 2 stomachs were "gorged" to the point of bursting on cutting the abdomen.
[3] Out of 18, 8 stomachs were "gorged" to the point of bursting on cutting the abdomen.
[4] The last column shows the number of stomachs in which dominance of one type of food over the others was clearly displayed, and its relation to the total in percent.

TABLE 2. *Frequency of occurrence of components of anchovy stomach contents, Monterey Bay, central California, collected in May, 1965. Of 139 stomachs in 9 samples, 26 were empty, 73 very poor, 5 poor, 17 half-filled, 2 filled to ¾ capacity, and 16 to capacity (2 being "gorged"). Dominance of one type of food over the others was found in 81 stomachs.*

Description	*Frequency of occurrence*			
	Dominating	*Second Place*	*Insignificant*	*Total*
	(Number and Percent)			
Copepods: large	–	–	1	1
small	–	–	8	8
microcalanids	–	–	1	1
eggs	–	–	15	15
fleshy parts	–	–	6	6
Mysids	–	–	1	1
Shrimps, small adults	–	–	2	2
Crustacean eggs (?)	–	–	11	11
fleshy parts (?)	19 (23.46%)	2	16	37
remains (?)	11 (13.58%)	–	–	11
Thaliaceans: *Salpa*	5 (6.17%)	6	16	27
Polychaete worms	–	–	1	1
Chaetognath worms	–	–	1	1
Hemicordata: *Enteropneusta* larvae	4 (4.94%)	2	29	35
Fish larvae	–	–	1	1
Pteropods: *Limacina* sp.	–	–	1	1
Medusae	–	–	1	1
Indeterminate fleshy material (?)	13 (16.05%)	14	3	30
Eggs (?)	–	–	1	1
Protozoans: Silicoflagellates	–	–	1	1
Algae (kelp-like) fragments	1 (1.23%)	–	4	5
Diatoms	28 (34.57%)	25	16	69
Anchovy scales (foreign matter)	–	–	8	8
Total	81 (100.00%)	49	144	274
Broken by Groups:				
Crustaceans	30 (37.04%)	2	61	93
Other zooplankters	9 (11.11%)	8	51	68
Indeterminate flesh and eggs	13 (16.05%)	14	4	31
	52 (64.20%)	24	116	192
Phytoplankton	29 (35.80%)	25	20	74
Foreign matter	–	–	8	8
Total	81 (100.00%)	49	144	274

Table 3. *Frequency of occurrence of components of anchovy stomach contents from northern Baja California, Mexico, collected in September, 1965. Of 409 stomachs in 29 samples collected, 35 were empty, 122 very poor, 127 poor, 26 filled to ¼ capacity, 40 half-filled, 33 filled to ¾ capacity, and 26 filled to capacity (2 being "gorged"). Dominance of one type of food over the others was found in 283 stomachs.*

Description	Frequency of occurrence				
	Dominating (number and percent)		Second Place	Insignificant	Total
Euphausiids: adult	40	14.14%	1	7	48
eggs	–	–	–	17	17
larvae	–	–	–	45	45
fleshy parts	8	2.82%	5	13	26
(mixed)—adult and fleshy parts	80	28.27%	4	5	89
	128	45.23%	10	87	225
Copepods: large	18	6.36%	10	43	71
small	1	0.35%	4	71	76
microcalanids	2	0.71%	–	100	102
small and microcalanids	11	3.89%	1	6	18
eggs	–	–	–	68	68
larvae	–	–	–	18	18
fleshy parts	20	7.06%	4	29	53
adult all types and flesh	47	16.61%	12	–	59
remains	1	0.35%	–	8	9
	100	35.33%	31	343	474
Other crustaceans:					
Mysids: adult	1	0.36%	–	7	8
larvae	–	–	–	3	3
(mixed)—adult and fleshy parts	2	0.71%	–	–	2
Amphipods: adult	2	0.71%	4	8	14
larvae in capsule	–	–	–	1	1
Isopods: adult	–	–	–	5	5
Cumaceans: adult	–	–	–	2	2
Porcellanid crab larvae	–	–	–	2	2
Hermit crab larvae	–	–	–	1	1
Brachyuran zoea	–	–	–	32	32
Brachyuran megalopa	–	–	–	16	16
Small shrimp, adults	–	–	–	2	2
Small shrimp, larvae	–	–	–	2	2
Ostracods	–	–	–	7	7
Balanus (cyprid stage) larvae	–	–	–	8	8
Cladocerans (*Podon*)	–	–	–	3	3
Unidentified crustacean larvae	–	–	–	6	6
Crustacean fleshy parts	6	2.11%	–	–	6
	11	3.89%	4	105	120

TABLE 3 (*Continued*)

Description	*Frequency of occurrence*				
	Dominating (number and percent)		*Second Place*	*Insignificant*	*Total*
Pelagic worms:					
Sagitta	–	–	–	10	10
Other Chaetognaths	1	0.36%	–	14	15
Polychaetes, adult	10	3.53%	6	12	28
Polychaetes, eggs	–	–	–	7	7
Polychaetes, larvae	–	–	–	9	9
Polychaetes, egg pouches and eggs	–	–	–	2	2
Hemichordata (*Enteropneusta*) larvae	–	–	1	62	63
Nemertean worms (pelagic stage)	–	–	–	2	2
	11	3.89%	7	118	136
Mollusca:					
Pteropods (*Limacina* sp.)	–	–	–	18	18
Heteropods	–	–	–	3	3
Gastropod larvae	–	–	–	8	8
Bivalve larvae	–	–	–	12	12
Cephalopods: squid larvae	–	–	–	20	20
Cephalopods: octopus larvae	–	–	–	2	2
	–	–	–	63	63
Vertebrates:					
Fish eggs	–	–	–	19	19
Fish eggs with larva inside	–	–	–	2	2
Fish larvae	4	1.43%	–	7	11
Fish remains	3	1.06%	2	6	11
Anchovy eggs	–	–	–	1	1
Anchovy eggs with larva inside	–	–	–	1	1
	7	2.49%	2	36	45
Other zooplanktonic forms:					
Cephalocordate larvae	–	–	–	8	8
Protozoans: Tintinnids	–	–	–	9	9
Protozoans: Foraminiferans	–	–	–	3	3
Protozoans: Radiolarians	–	–	–	4	4
Protozoans: Silicoflagellates	–	–	–	1	1
Hydroid, chunks	–	–	–	1	1
Appendicularians (*Oikopleura*)	5	1.75%	6	57	68
Thaliaceans: (*Salpa*)	3	1.06%	4	84	91
Thaliaceans: (*Salpa*) with embryo	–	–	–	7	7
Thaliaceans: Doliolids	–	–	–	8	8
Bryozoan "cyphonautes" larvae	2	0.71%	5	72	79

Table 3 (*Continued*)

Description	*Frequency of occurrence*				
	Dominating (number and percent)		*Second Place*	*Insignificant*	*Total*
Jellyfish (medusae, ctenophores, etc.)	–	–	–	19	19
Echinoderms: sea cucumbers	–	–	1	10	11
sea urchin parts	–	–	–	1	1
Brachiopod larvae	–	–	–	3	3
	10	3.52%	16	287	313
Phytoplankton:					
Diatoms ("present" only)	–	–	–	65	65
Dinoflagellates ("present" only)	–	–	–	19	19
Algae (*Phaeocystis*)	–	–	–	6	6
Algae tissues (kelp-like)	–	–	–	45	45
	–	–	–	135	135
Unidentified material:					
Fleshy parts (?)	12	4.24%	–	41	53
	12	4.24%	–	41	53
Foreign matter:					
Insect	–	–	–	1	1
Fine sand grains	1	0.35%	–	27	28
Fine mica flakes	–	–	1	24	25
Fine sand and mica, mixed	3	1.06%	12	8	23
Minute pebbles	–	–	–	2	2
Pollen grains	–	–	–	1	1
Fish scales	–	–	–	1	1
	4	1.41%	13	64	81
Parasites: Nematodes	–	–	–	18	18
Total	283	100.00%	83	1297	1663
Broken by groups:					
Crustaceans, all	239	84.45%	45	535	819
Other zooplanktonic forms	28	9.90%	25	504	557
Indeterminate fleshy matter	12	4.24%	–	41	53
Total, zooplanktonic material	279	98.59%	70	1080	1429
Phytoplankton	–	–	–	135	135
Foreign matter	4	1.41%	13	64	81
Grand Total	283	100.00%	83	1281	1645
Parasites	–	–	–	18	18

plankton (6.59 percent), and the last place was taken by foreign matter (only 0.60 percent) (fig. 2).

As to predation of the northern anchovy on small fish, analysis of stomach contents revealed 104 cases of fish eggs and larvae, mostly of its own kind. In 8 cases these items were found to be the major food, 3 times they occupied second place, and 93 times they were present in meager quantities. Baxter (1967) also observed this pattern. Among crustaceans found in dominating volumes in the stomach contents, the first place belongs to copepods and the second to euphausiids (all developmental stages from egg to adult form in both groups).[2]

The same trend is illustrated in table 9 which shows food-type incidence in 840 filled stomachs (recapitulation of tables 2 through 7) regardless of the quantity of food present in the stomach. In this case, out of 98 food type entries on the menu of our anchovy, only 11 represented phytoplankton and foreign matter. By contrast zooplankters constituted 86.54 percent, of which 50.78 percent were crustaceans. In the latter group, copepods were again most abundant (29.32 percent),[3] while the euphausiids were second in frequency (9.54 percent). Incidence of each of the rest of the 24 forms of crustaceans was very low. The phytoplankters made up only 10.99 percent of the total (fig. 3).

OBSERVATION ON FEEDING BEHAVIOR

From actual visual observations both in the field and in the tanks of Steinhart Aquarium, and from the examination of the stomach contents, it is clearly evident that the northern anchovy in all size categories is both a filter feeder and a particulate feeder,[4] depending on the size of the available food organisms (Miller, 1967, 1968). As an example of filter feeding, reference is made to a field observation of the writer recorded on September 26, 1965, at San Jose Point in Baja California, which reads as follows:

"... at 9:00 A.M. a huge school of juvenile anchovies around anchored *Alaska* was actively feeding on some microplanktonic organisms very close to the surface. For two hours we watched this interesting behavior. Water was very clear and we could see all movements and feeding pattern of the school. It was a sort of a loose formation in which individual members were sparsely located, however all being orientated toward east. With mouths wide open and gill-covers stretched out, they strained water. They did this while rising toward the surface in a rhythmic wave-like pattern. When they headed down, they closed their mouths and tightly pressed gill-covers to the gills, as if they were swallowing organisms trapped by gill-rakers. With line and treble hook I snagged 12 young fish 67–91 mm. standard length."

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[2] Baxter (1968) recorded euphausiids as the most common food object in the stomach contents of the anchovies collected at night. It can be added that this is especially true when electric light and blanket net are used as collecting gear.

[3] A list of partially identified copepods is presented in appendix A.

[4] Experimental studies, conducted at the California Current Resources Laboratory of the U.S. Bureau of Commercial Fisheries in La Jolla, revealed that predation is by filtering on organisms less than 1 mm. in length and by particulate biting on organisms a few mm. in length. The larger organisms are preferred. (Anonymous, 1967).

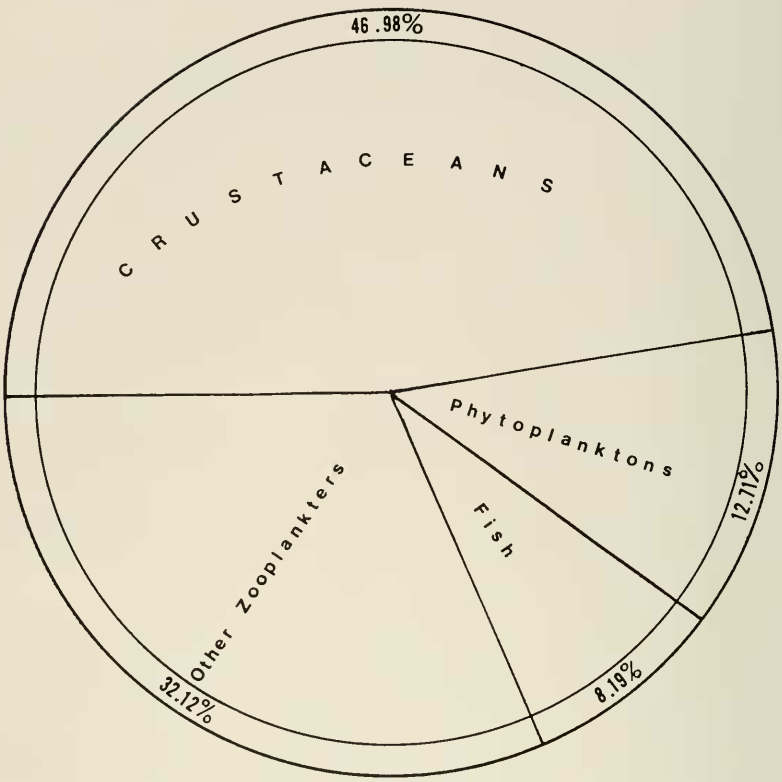

Figure 4. Percentage frequency of occurrence of various types of organisms found in the stomachs of 273 sardines in relation to total number of occurrences. Based on table 1 of Cadet H. Hand and Leo Berner, Jr. (1959).

Later, stomach contents of these fish were examined in the laboratory. Ten of them were filled up to ¾ capacity, and 2 were "poor" in contents. Their stomachs contained small copepods, microcalanids, copepod eggs and nauplii, and bryozoan "cyphonautes" larvae. Diatoms (*Coscinodiscus* species) were also present in 5 stomachs, but in very insignificant numbers. Selective or particulate feeding also was observed in the sea many times, usually when electric light at night was used as attractant and blanket net as catching gear. As an example, a record is given below dated October 19, 1966, for night anchorage of the *Alaska* in Government Cove (near Santa Barbara):

". . . About 11:00 P.M. Alaska dropped her anchor in Government Cove (southern California). A 1500-watt lamp was suspended from the boom about 12 feet above the water surface. Soon after midnight swarms of planktonic organisms appeared within the illuminated

zone. Large euphausiids, chaetognaths, large copepods, and many kinds of other smaller organisms were abundantly represented. About 2:00 A.M. a school of anchovies made its appearance, and after a while a wild chase started. The illuminated area seemed boiling. The fish feeding on the surface uninterruptedly splashed water with their tails. There was a "disorderly pattern" of feeding; it seemed that each member of the school acted individually, swimming back and forth, and up and down, and attacking its prey and snapping at it at irregular short-time periods. The fish were so wildly "preoccupied" with their chase that I had no difficulty in catching them with a scoop net. Twelve anchovies 135–145 mm. standard length were so obtained. Two of the stomachs were ¾ filled, while the rest were simply "gorged," and when cutting the abdomens the stomachs "blew up," pouring the contents on the table."

Examination of the contents later in the laboratory disclosed that euphausiids were the dominating food component in all 12 stomachs. They represented 75 percent to 95 percent of the wet volume of the contents in the individual stomachs. Their numbers varied from 11 to 15 in the stomachs filled up to ¾ capacity, and from 38 to 180 (including young and larvae) in the stomachs filled to extreme capacity ("gorged"). Second place was occupied mostly by the euphausiid soft parts (8 times), 3 times by large copepods, and once by a polychaete worm broken to pieces. Many other zooplankters of smaller size, found in the stomach contents in meager numbers, might have been ingested by the anchovy while feeding on larger animals. No diatoms were found at all.

Visual observations on feeding behavior of the schools of northern anchovy and Pacific sardine kept in the past for experimental purposes in the 1000-gallon tanks of the Steinhart Aquarium, revealed the very same dual tendency in feeding patterns of these 2 species. When live brine shrimps, *Artemia salina*, were added to the tank, the school (sardines or anchovies alike) would rush at the dense cloud of shrimps, disperse them at once, and then begin to snap up the individual animals. When just-hatched brine shrimps were added to the tank, the sardines or the anchovies would proceed with filter-feeding. Again, when these fishes were fed with finely chopped or ground horse heart, ground fish, or commercially manufactured dry fish pellets containing protein, they demonstrated ability to turn to particulate feeding. The examination of the contents of the entire set of stomach collections described above exposed a great diversity of food objects on the menu of the anchovy. It became evident that it feeds on many types of planktonic organisms, both of animal and plant origin. This examination of the components of the stomach contents confirmed once again that the anchovy is both a filter feeder and a particulate one.

In addition to this, an observation was made during the present study which may indicate an aggressive character in the feeding behavior of the anchovy. In several stomachs of a single sample there were found chunks of larger polychaete worms, a fact that may suggest the possibility of a group attack by several anchovies on a larger animal which they tore to pieces, a single fish being unable to swallow the entire worm.

Table 4. *Frequency of occurrence of components of the anchovy stomach contents from northern Baja California, Mexico, and southern California waters collected in October, 1966. Of 220 stomachs in 21 samples collected, 23 were empty, 21 very poor, 53 poor, 44 filled to ¼ capacity, 37 half-filled, 24 filled to ¾ capacity, and 18 to full capacity (8 being "gorged"). Dominance of one type of food over the others was found in 165 stomachs.*

Description	Frequency of occurrence				
	Dominating (number and percent)		Second Place	Insignificant	Total
Euphausiids: Adult	37	22.43%	9	23	69
eggs	–	–	–	9	9
larvae	–	–	–	17	17
fleshy parts	1	0.60%	24	17	42
(mixed)—adult and fleshy parts	21	12.73%	1	–	22
	59	35.76%	34	66	159
Copepods: large	3	1.83%	19	52	74
small	6	3.64%	4	98	108
microcalanids	–	–	2	85	87
eggs	–	–	–	72	72
larvae	–	–	–	35	35
Herpacticoid adult	–	–	–	1	1
fleshy parts	29	17.57%	12	38	79
(mixed)—large adult and fleshy parts	4	2.42%	–	–	4
(mixed)—small adult and fleshy parts	9	5.45%	2	–	11
	51	30.91%	39	381	471
Other Crustaceans:					
Mysids: adult	1	0.60%	5	11	17
larvae	–	–	–	4	4
Amphipods: adult	2	1.21%	7	44	53
larvae in capsules	–	–	–	6	6
Phyllopods (Spiny lobster larvae)	–	–	–	4	4
Isopods: adult	–	–	1	11	12
Porcellanid crab larvae	–	–	–	10	10
Hermit crab larvae	–	–	–	6	6
Sand crab larvae	–	–	–	1	1
Brachyuran zoea	–	–	–	45	45
Brachyuran megalopa	–	–	–	35	35
Coridean shrimp	–	–	–	1	1
Small shrimp	–	–	–	1	1
Sergestid shrimp larvae	–	–	–	1	1
Ostracods	1	0.61%	–	12	13
Balanus (cyprid stage) larvae	–	–	–	9	9
Cladocerans (*Podon*)	–	–	–	10	10
Crustacean eggs (?)	–	–	–	1	1
Crustacean larvae (?)	–	–	–	24	24

TABLE 4 (*Continued*)

Description	*Frequency of occurrence*				
	Dominating (number and percent)		*Second Place*	*Insignificant*	*Total*
Crustacean fleshy parts (?)	6	3.64%	1	5	12
Crustacean remains	3	1.82%	–	1	4
	13	7.88%	14	242	269
Pelagic worms:					
Sagitta	–	–	–	9	9
Other chaetognaths	–	–	–	8	8
Polychaete adults	8	4.85%	3	25	36
eggs	–	–	1	2	3
larvae	–	–	–	3	3
egg pouch with eggs	2	1.21%	–	–	2
fleshy chunks	1	0.60%	2	–	3
Hemichordata (*Enteropneusta*) larvae	–	–	–	35	35
	11	6.66%	6	82	99
Mollusca: Pteropods (*Limacina* sp.)	–	–	–	40	40
Heteropods	1	0.61%	–	9	10
Gastropod larvae	–	–	–	11	11
Bivalve larvae	–	–	–	5	5
Cephalopod larvae	–	–	–	9	9
	1	0.61%	–	74	75
Vertebrates:					
Fish eggs	–	–	1	35	36
larvae and fish flesh	–	–	–	7	7
post-larval stage	1	0.61%	–	–	1
Anchovy eggs	–	–	–	1	1
with larva inside	–	–	–	1	1
	1	0.61%	1	44	46
Other zooplanktonic forms:					
Protozoans:					
Tintinnids	–	–	–	9	9
Dictocystis	–	–	–	1	1
Salpiginella	–	–	–	2	2
Parafavella	–	–	–	1	1
Ciliates	–	–	–	3	3
Foraminiferans	–	–	–	1	1
Radiolarians	2	1.21%	–	20	22
Silicoflagellates	–	–	–	2	2
Appendicularians:					
Oikopleura	13	7.88%	7	54	74
Fritillaria	–	–	–	1	1

Table 4 (*Continued*)

Description	Frequency of occurrence: Dominating (number and percent)		Second Place	Insignificant	Total
Thaliaceans:					
Salpa	9	5.45%	10	85	104
with embryos	1	0.61%	1	5	7
with aggregates	2	1.21%	1	–	3
Doliolids	–	–	–	13	13
Bryozoan "cyphonautes" larvae	–	–	–	30	30
Jellyfish (medusae, ctenophores, etc.)	–	–	–	31	31
Echinoderm larvae (sea urchins)	–	–	–	6	6
Echinoderm adult (sea cucumbers)	–	–	–	2	2
	27	16.36%	19	266	312
Indeterminate zooplanktonic matter:					
Fleshy soft parts (?)	2	1.21%	–	4	6
Eggs (?)	–	–	–	14	14
Larvae (?)	–	–	–	4	4
	2	1.21%	–	22	24
Phytoplankton:					
Diatoms	–	–	1	75 (pr.)	76
Dinoflagellates	–	–	–	27 (pr.)	27
Algae: *Phaeocystis*	–	–	–	4 (pr.)	4
tissue (fragments of kelp-like algae)	–	–	–	25	25
	–	–	1	131	132
Foreign matter:					
Fish scales	–	–	–	1	1
Fine sand grains	–	–	–	6	6
Fine mica flakes	–	–	–	2	2
	–	–	–	9	9
Parasites:					
Nematodes	–	–	–	3	3
Total	165	100.00%	114	1320	1599
Broken by groups:					
Crustaceans, all	123	74.55%	87	689	899
Other zooplanktonic forms	40	24.24%	26	466	532
Indeterminate fleshy material	2	1.21%	–	22	24
Total zooplanktonic material	165	100.00%	113	1177	1455
Phytoplankton	–	–	1	131	132
Foreign matter	–	–	–	9	9
Grand total	165	100.00%	114	1317	1596
Parasites	–	–	–	3	3

Abbreviation: pr. = present.

Table 5. *Frequency of occurrence of components of anchovy stomach contents from northern Baja California, Mexico, collected on June 12, 1965, by Dr. Reuben Lasker. Of 20 stomachs in collection, 1 was empty, 2 poor, 7 half-filled, 4 filled to ¾ capacity, and 6 filled to full capacity. Dominance of one type of food over the others was found in 18 stomachs.*

Description	*Frequency of occurrence*			
	Dominating	*Second Place*	*Insignificant*	*Total*
	(*Number and Percent*)			
Euphausiids: Adult	–	1	1	2
fleshy parts	1 (5.56%)	–	–	1
Copepods: large	–	–	1	1
small	–	–	1	1
microcalanids	–	–	1	1
eggs	–	–	8	8
larvae	–	–	1	1
Crustacean soft parts (?)	2 (11.11%)	–	2	4
Hemichordata: *Enteropneusta* larvae	–	–	3	3
Protozoans: Tintinnids	–	–	11	11
Indeterminate fleshy material	–	–	2	2
Diatoms	15 (83.33%)	2	2 (pr.)	19
Dinoflagellates	–	1	1 (pr.)	2
Total	18 (100.00%)	4	34	56
Broken by groups:				
Crustaceans	3 (16.67%)	1	15	19
Other zooplankters	–	–	14	14
Indeterminate fleshy material	–	–	2	2
Phytoplankton	15 (83.33%)	3	3	21
Total	18 (100.00%)	4	34	56

Abbreviation: pr. = present.

As to the phytoplankton in relation to 840 filled stomachs (926 minus 86 empty), diatoms were found in 295, taking dominating position in 43 cases, second place in 64, and being present in insignificant quantities in 188. Dinoflagellates once took second place and 67 times were recorded as "present." Algae and algal tissues of kelp-like type were found once in dominating position, and 85 times were present in insignificant quantities. In certain collections, diatoms consumed by the anchovy played a very important role in its diet.

In the stomach collection from Monterey Bay, made in the month of May, 1965, dominance of diatoms over the other food types was equivalent to 34.57 percent of the total. Several stomachs were filled to capacity and because of uniform food components the stomachs were of green color. In some of these stomachs, diatoms were the only food item found, and quite often 99 percent of the diatoms in such stomachs belonged to a single form (*Chaetoceros* species, for instance).

In the Monterey collection, the anchovy ranged in size from 85 mm. to 215 mm. standard length, and diatoms were present in all size groups (85–100, 100–150, 160–215). In certain samples they were present in every stomach in various quantities. In other stomachs of this Monterey collection phytoplankters and zooplankters were present more or less in equal amounts, but in a much greater number of cases, only a few specimens of diatoms were found. Dinoflagellates were recorded in meager quantities.

In Dr. Lasker's collection from Bahia Soledad made in the month of June, 1965, diatoms were found in 19 out of 20 stomachs—in 15 cases they were first in abundance, twice they took second place, and twice they were present in insignificant quantities. In some stomachs the contents were composed of diatoms exclusively, or diatoms with a small admixture of dinoflagellates. Among 11 generic forms of diatoms recorded from this collection, *Chaetoceros*, *Coscinodiscus*, and *Thalassiosira* were most numerous.

An explanation for the abundance of diatoms in the anchovy stomachs from Monterey, and from Bahia Soledad as well, may be found in the observations of Abbott and Albee (1967) on seasonal distribution of phytoplankton in Monterey Bay. They stated that "for the thirteen-year period, 1954–1966, maximum crops appeared most frequently in June, but in different years peaks fell in all months from March through July." They maintain that *Chaetoceros* "is usually the predominant genus in the Bay in spring and early summer." This explains why in our collection certain stomach contents were composed of diatoms of the genus *Chaetoceros* in amounts up to 99 percent of the total. Again, in the Bahia Soledad collection, *Chaetoceros* was dominant among the 11 forms of diatoms recorded for the said collection.[5]

In studying behavioral responses of the northern anchovy to various intensities of white light under laboratory conditions at the California Academy of Sciences, (Loukashkin and Grant, 1965), it was found that the fish always displayed preference for the lower intensity regardless of any combination of the values of contrasting light intensity zones in the experimental tank. Therefore, similar behavior was expected of the anchovy in its natural habitat. Field observations made by the present writer, and by observers on the staff of the California State Fisheries Laboratory of the Department of Fish and Game, often expressed in their Cruise Reports, confirmed this natural response of the anchovy. In bright sunshine schools of anchovies as a rule descend to deeper layers of water than they do in overcast weather or at times when upper layers of water are full of plankton, which would provide both a filter from the sunlight and a source of food.

Presence of bottom-dwelling animals, such as certain foraminiferans, worms,

[5] For a complete list of diatoms and dinoflagellates identified chiefly by Dr. G Dallas Hanna, see appendix B.

FIGURE 5. Stomach contents of the northern anchovy no. 124 collected on September 27, 1965, 4–5 miles WNW. of Soledad Rock in Baja California, Mexico.

Stomach of this 136 mm. fish (standard length) was filled with food to capacity, and its contents consisted exclusively of adult and juvenile euphausiids and their parts (84) with 3 large copepods.

Only a part of the contents is shown in this picture, being greatly magnified. Picture courtesy of Mr. Allyn G. Smith, California Academy of Sciences, April, 1969.

and amphipods, and an accumulation of fine sand grains and mica flakes (even tiny pebbles) in the anchovy stomachs demonstrated that this fish not infrequently descends to near-bottom layers, especially in shallower waters, and behaves there apparently as an indiscriminate filter feeder. Referred to a category of foreign matter in figures and tables, sand grains, mica flakes, and these 2 materials mixed together were found in 85 stomachs in different samples, being present in dominating volumes on 4 occasions, taking second place 13 times, and recorded in insignificant quantities 68 times.[6]

Within the group of foreign matter, pollen grains were included on the basis of a single occurrence in stomach no. 714 from anchovy collected near Point Dume on September 14, 1966. Presence of pollen in the stomachs of planktophagous species has been recorded for anchoveta and sardine: Bayliff (1963)

[6] For instance, in the sample VIII, taken on September 21, 1965, at 6:00 P.M. in San Quintin Bay, 12 stomachs were filled from "poor" to "½ capacity." Presence of sand grains and mica flakes was noted in all of them: in dominant position in four, in second place in two, and in insignificant quantities in three.

Table 6. *Frequency of occurrence of components of anchovy stomach contents from northern Baja California, Mexico, collected by Dr. Reuben Lasker on October 20 and 27, 1965. Of 40 stomachs in the collection, 2 were very poor, 18 poor, 19 half-filled, and 1 filled to capacity. Dominance of one type of food over the others was found in 23 stomachs.*

Description	Frequency of occurrence			
	Dominating	Second Place	Insignificant	Total
	(Number and Percent)			
Euphausiids: eggs only	–	–	1	1
Copepods: large	–	–	3	3
small	–	–	4	4
microcalanids	–	–	3	3
eggs	–	–	4	4
fleshy parts	20 (86.95%)	–	–	20
Amphipods	–	–	1	1
Thaliaceans: *Salpa*	–	–	2	2
Appendicularians: *Oikopleura*	–	–	2	2
Hemichordata: *Enteropneusta* larvae	–	–	2	2
Chaetognaths: *Sagitta*	–	–	1	1
Fish egg shell	–	–	1	1
Jellyfish larvae	–	–	1	1
Protozoans: Tintinnids	–	1	3	4
Radiolarians	–	–	1	1
Silicoflagellates	–	–	1	1
Indeterminate fleshy material	3 (13.05%)	–	16	19
Diatoms	–	3	10 (pr.)	13
Dinoflagellates	–	–	2	2
Total	23 (100.00%)	4	58	85
Broken by groups:				
Crustaceans	20 (86.95%)	–	16	36
Other zooplankters	–	1	14	15
Indeterminate fleshy material	3 (13.05%)	–	16	19
Phytoplankton	–	3	12	15
Total	23 (100.00%)	4	58	85

Abbreviation: pr. = present.

found pollen grains in the diet of the anchoveta, *Cetengraulis mysticetus*, from the Gulf of Panama; Gaïl (1936) observed adult Japanese sardines in the USSR territorial waters of the Sea of Japan actively feeding on pollen grains of the Korean pine, *Pinus koraiensis*, (which he classified as "pseudoplankton"). During the blooming season he found sardine stomachs filled with masses of this pollen, rendering the stomachs bright yellow in color. It would be of interest to know if such a mass appearance of pollen on the surface of inshore waters in

the California Current system has ever taken place, and how this supply has been utilized by the anchovy and other planktophagous fish.

It is not unlikely that, if a greater number of stomachs were obtained, all the components of the plankton in the anchovy's environment could be found in its intestinal tract, save for the extremely minute planktonic forms and those too large for it to ingest. The sampling problem inherent in food studies is usually inadequacy of the sampled material. Better definition of general food habits of any animal species would require the use of a greater number of stomachs. Hand and Berner (1959) listed 34 food objects found in the stomachs of 273 Pacific sardines. In our 6 collections numbering 926 stomachs the list of food items recorded reached 96, including all 34 found by them, or approximately threefold. These results are almost in direct proportion to the number of stomachs examined. And yet, the present writer does not believe that the material collected presents a complete picture of the food habits of the anchovy. Therefore, he considers his account a preliminary one until more abundant data have been accumulated and reported. Nevertheless, despite a limited number of stomachs in the collections taken sporadically and randomly within the area of California Current System, it is clearly seen that the anchovy feeds indiscriminately on a variety of planktonic organisms available within the area occupied.

The other planktophagous pelagic fish occurring in the vicinity, or mixed with the anchovy schools, would certainly feed on the same plankton available to the anchovy. This was well demonstrated in the catches of mixed lots of fish during the author's collecting cruises aboard M/V *Alaska* in 1965 and 1966. On September 21, 1965, at 10:15 P.M., using an electric light as attractant and the blanket net as fishing gear, in San Quintin Bay, Baja California, 2.8 miles offshore in waters 17 fathoms deep, 3 species of pelagic fish were caught at a single operation. Among them were 3,000 jack mackerel, *Trachurus symmetricus*, 200 Pacific sardines, and 10 anchovies. All 10 stomachs of the latter were filled to capacity mostly by large copepods, with insignificant amounts of other zooplankters. Examination of stomach contents of 11 randomly picked sardines (3 stomachs were filled to extreme capacity—"gorged," 2—¾ capacity, 2—½ capacity, and 4 were poor in contents) revealed identical food items in the same proportions (appendix C). In 12 stomachs of the jack mackerels 7 were filled to full capacity, 2 to ¾ capacity, and 3 to ½ capacity. The dominating food item was large copepods, with euphausiids taking second place (appendix D). In sample LVIII taken on October 18, 1966, at 8:13 P.M. near Point Conception, southern California, 4 miles offshore, 7 anchovies and 2 hake, *Merluccius productus*, were caught in the midwater trawl. In 3 out of 7 anchovies selected (nos. 783, 785, and 788), euphausiids were in dominating position; the stomachs of the other three were filled with copepods, salps, and polychaete worms; and the seventh stomach was empty. The hake stomachs were filled with euphausiids

alone[7] (appendix E). The above examples may serve as a basis for the generalization that certain, if not all, pelagic fishes regarded as planktophagous in their food habits are indiscriminate omnivorous animals.

As to the northern anchovy, the same examples present a clear picture of existence of interspecific food competition.[8]

Just about at the outset of the present study, when no exact information on the food of the adult anchovy existed, Murphy (1966) published his exhaustive analysis of the population biology of the Pacific sardine in the California Current System. In discussion of the increase of anchovy population concurrent with simultaneous decrease of that of the Pacific sardine, he stated his personal impression that these 2 species "eat about the same things," and therefore it was hypothetically reasonable to consider anchovy and sardine "fundamental competitors." This impression and postulation appear to be correct.

Berner (1959), in his report on food studies of the larvae of the northern anchovy said that larvae longer than 7 mm. "actually ate the greatest variety of food."[9] The major food item in all larval groups consisted of crustaceans in various developmental stages, of which copepods were most important. Copepod eggs and nauplii were met with most frequently and most abundantly. The other items found in the stomachs were adult copepods, euphausiid eggs and nauplii, clam larvae, ciliates, dinoflagellates, tintinnids, coccolithophores, foraminiferans, unidentified eggs, miscellaneous plant material, and miscellaneous unidentified material.

Shumann (1963) in reference to findings by D. K. Arthur[10] states that food of the larvae of northern anchovy, Pacific sardine, and jack mackerel is "substantially the same."

From Berner and Schumann's studies, and from our investigations as well, it appears that the northern anchovy in all age stages remains a planktophagous animal, and that it is located in a low trophic level, near the primary production link. For the Japanese anchovy, *Engraulis japonica,* according to Kubo (1961) and Hayasi (1967), copepods comprise the major food throughout the life span. The size of the food objects is linearly correlated with the size of the fish. Nakai *et al.* (1962) provided more specific details. They found out that "postlarvae of less than 5 mm. total length, just after absorbing yolk, take mainly eggs and

[7] Euphausiids are abundant and important organisms in the ocean plankton available to a variety of planktophagous pelagic fishes, "ranging from sardine and jack mackerel to tunas and salmon, and they are the chief food of baleen whales" ((Anonymous, 1967). To this listing we may add our anchovy, hake, Pacific herring, *Clupea harengus pallasi,* (Mikulich, 1960), and Argentine anchovy (de Ciechomski, 1967).

[8] In addition to sardine, jack mackerel, and hake as anchovy competitors, we may include juvenile sablefish, *Anoplopoma fimbria,* which, according to Conway *et al.* (1968), feeds "primarily on small pelagic organisms, including copepods, amphipods, euphausiids, and the urochordate, *Oikopleura* sp." They characterize sablefish at all ages, including juveniles, as "highly opportunistic in feeding habits, ingesting whatever suitable prey species are most abundant or available in their immediate surroundings."

[9] Berner examined 13,620 larvae of which only 211 had ingested food.

[10] "The particulate food and food resources of the larvae of three pelagic species, especially the Pacific sardine, *Sardinops caerulea.*" Doctoral thesis, University of California, Scripps Institution of Oceanography, 231 pp. (typewritten), 1956.

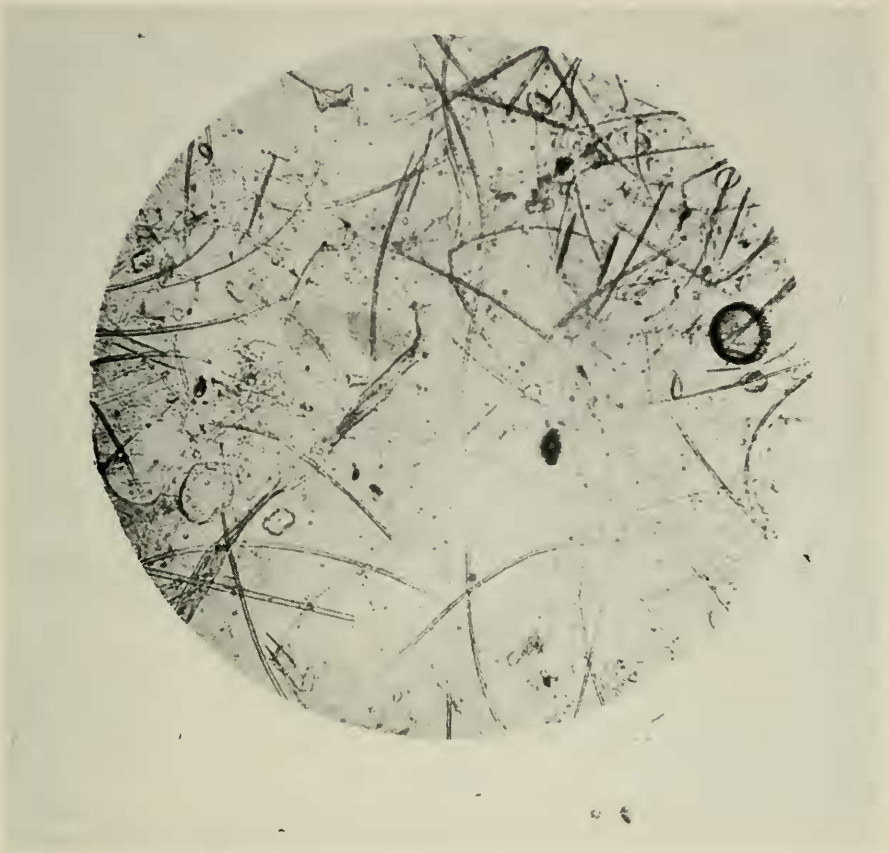

Figure 6. Photomicrograph of diatoms from the contents of the stomachs of the northern anchovy (*Engraulis mordax*) nos. 544–553. The slender spines are from various species of *Chaetoceros*. The dark circle on the right is *Stephanopyxis turris*.

Monterey Bay, California, May 27, 1965. The diatoms were the chief item in the stomach contents (from 90–100 percent) rendering bright green color to the stomach.

Photograph by Dr. G Dallas Hanna, California Academy of Sciences, June, 1969.

nauplii of copepods. Only a few of them were found with protozoans, small mollusca, and diatoms in their digestive tracts. Postlarvae of 5–10 mm. total length still mainly eat nauplii of copepods, but copepodid larvae increase in number from before. Generally, sizes of postlarvae and food organisms are correlated with each other. Number of postlarvae with food in the digestive tract occupy less than 20 percent on the average. They take the food most actively in the day time."[11] The juveniles through adult stages (Nakai *et al.*,

[11] The same is true of the Black Sea anchovy, *Engraulis encrasicholus* (Duka, 1961).

Table 7. *Frequency of occurrence of components of anchovy stomach contents from southern California waters collected by Mr. Deon L. Hamilton in January–February, 1968. Of 98 stomachs in 7 samples collected, 1 was empty, 94 poor, and 3 half-filled. Dominance of one type of food over the others was found in 97 stomachs.*

Description	Frequency of occurrence				
	Dominating (number and percent)		Second Place	Insignificant	Total
Euphausiids: adult	–	–	–	1	1
eggs	–	–	–	1	1
Copepods: large	–	–	2	18	20
small	–	–	4	34	38
microcalanids	–	–	–	38	38
eggs	–	–	–	17	17
larvae	–	–	–	8	8
fleshy parts	34	35.05%	–	–	34
(mixed)—adult and fleshy parts	20	20.62%	–	–	20
	54	55.67%	6	117	177
Other crustaceans: Amphipod larvae	–	–	–	2	2
Cumacean adult	–	–	–	1	1
Brachyuran megalopa	–	–	–	1	1
Porcellanid crab larvae	–	–	–	2	2
Small shrimp larvae	–	–	–	2	2
Sergestid shrimp larvae	–	–	–	1	1
Balanus (cyprid stage) larvae	–	–	–	3	3
Crustacean larvae (?)	–	–	–	10	10
Crustacean fleshy parts (?)	10	10.31%	–	–	10
	10	10.31%	–	22	32
Pelagic worms:					
Sagitta	–	–	–	1	1
Polychaete worm	–	–	1	2	3
Nemertean worm larvae (pelagic stage)	–	–	–	1	1
Hemichordata: *Enteropneusta* larvae	–	–	–	50	50
	–	–	1	54	55
Mollusca:					
Pteropods (*Limacina* sp.)	–	–	–	1	1
Bivalve larvae	–	–	–	2	2
Cephalopod larvae	–	–	–	2	2
	–	–	–	5	5
Vertebrates:					
Fish eggs	–	–	–	11	11
	–	–	–	11	11

TABLE 7 (continued)

Description	*Frequency of occurrence*				
	Dominating (number and percent)		*Second Place*	*Insignificant*	*Total*
Other zooplanktonic forms:					
Protozoans—Tintinnids	–	–	–	2	2
Radiolarians	–	–	–	6	6
Appendicularians—*Oikopleura*	–	–	–	7	7
Thaliaceans—*Salpa*	–	–	–	10	10
Jellyfish	–	–	–	7	7
Bryozoan "cyphonautes" larvae	–	–	–	2	2
	–	–	–	34	34
Unidentified zooplankton:					
Fleshy material (?)	33	34.02%	–	–	33
Eggs (?)	–	–	–	8	8
	33	34.02%	–	8	41
Phytoplankton:					
Diatoms	–	–	33 (v.m.)	10 (m.) 10 pr.	53
Dinoflagellates	–	–	–	18 pr.	18
Algae tissues (kelp type)	–	–	–	1	1
	–	–	33	39	72
Foreign matter:					
Fish scales	–	–	–	2	2
Fine sand grains	–	–	–	1	1
	–	–	–	3	3
Parasites:					
Nematodes	–	–	–	1	1
Total	97	100.00%	40	294	431
Broken by groups:					
Crustaceans	64	65.98%	6	139	209
Other zooplanktonic forms	–	–	1	104	105
Unidentified zooplanktonic material	33	34.02%	–	8	41
Phytoplankton	–	–	33	39	72
Foreign matter	–	–	–	3	3
Total	97	100.00%	40	293	430
Parasites	–	–	–	1	1

Abbreviations: v.m. = very many; m. = many; pr. = present.

1955, and Kubo, 1961) are also dependent on copepods. Other food organisms are diatoms, various types of small crustaceans, larval mollusks, chaetognaths, and other small animals. The adult Japanese anchovy eats eggs and larvae of fishes including its own, as is the case with our anchovy.

Table 8. *Frequency of occurrence of dominating food types in 667 anchovy stomachs.*

Group	*Description*	*Number*	*Percent*
Zooplankton—Crustaceans	Copepods, all stages, flesh	225	33.73
	Euphausiids, all stages, flesh	188	28.18
	Other crustaceans all stages, flesh	9[1]	1.35
	Indeterminate crustacean flesh	43	6.45
	Indeterminate crustacean remains	14	2.10
		479	71.81
Zooplankton—Vertebrates	Fish larvae	4	0.60
	Fish remains	4	0.60
		8	1.20
Zooplankton—Other animals	Protozoans: Radiolarians	2	0.30
	Appendicularians	18	2.70
	Salps	20	3.00
	Worms: Hemichordata larvae	4	0.60
	Chaetognaths	1	0.15
	Polychaetes	21	3.15
	Mollusca: Heteropods	1	0.14
	Bryozoa: Cyphonautes larvae	2	0.30
		69	10.34
Zooplankton—Indeterminate	Fleshy material	63	9.46
Total for Zooplankton		619	92.81
Phytoplankton	Diatoms	43	6.45
	Algae (kelp-like) tissues	1	0.14
Total for Phytoplankton		44	6.59
Foreign matter	Sand grains, mica flakes, etc.	4	0.60
Grand Total		667	100.00

[1] Mysids, Amphipods and Ostracods.

A detailed account on the food habits of larvae and juveniles of the Argentine anchovy, *Engraulis anchoita*, was recently published by de Ciechomski in 2 articles (1967a and 1967b). She stated that the basic food of fish 35–80 mm. long consists of copepods in all stages of development: eggs, nauplii, and adult forms. Their diet includes also juvenile decapods and other crustaceans, eggs of various marine organisms, and sometimes fish and mollusk eggs. In the stomach contents of juveniles of 40 mm. length she found radiolarians and acantharians, but in scarce amounts. In juveniles 50 mm. long there appeared diatoms and dinoflagellates, always with zooplankters present. However, she referred to other investi-

FIGURE 7. Brown pelicans and sea-gulls feeding on a large school of anchovies (*Engraulis mordax*) at sunset in San Quintin Bay, Baja California. September 21, 1965.

gators whose findings were different from her own (Fuster de Plaza, 1964, and Angelescu and Fuster de Plaza, 1962). According to de Ciechomski, they found the stomach contents of the juveniles to be composed primarily of phytoplankton. In fish 50 mm. to 100 mm. they found a "predominance of diatoms," but as soon as juveniles approach the adult stage their diet becomes "preferentially zooplanktonic." According to the said investigators, in the stomachs of the fish 150–190 mm. long, copepods (especially calanids), pelagic amphipods, sergestid shrimps, and sometimes juveniles of anchovy and other fish compose the bulk of the contents. But contrary to the statement of the above mentioned authors, de Ciechomski in her own investigations disclosed a quite different situation. She found out that "the larvae and juveniles of the Argentine anchovy are zooplanktophagous from their earliest stages. The contribution of the phytoplankton to their diet is quite small." The diet of the adult fish is made up almost exclusively of zooplankters. The most important food items for larvae and juveniles 22–90 mm. long are "various groups of Copepoda, especially the Calanoida"; and least in importance are Cyclopoida.[12] Second in order of

[12] Among calanids the most frequently encountered forms were *Paracalanus parvus* and *Centropages* spp., and among cyclopoids—*Oithona minuta* and *Corycaeus* spp. Herpacticoid copepods were represented only by a single species—*Eutherpina acutiformis*. The calanids and herpacticoid copepods frequently and abundantly found in the stomach contents of the larval and juvenile Argentine anchovy were the most abundant forms in the plankton samples taken concurrently.

Table 9. *Food type incidence in 840 filled stomachs of northern anchovies collected in 1965–1968 in northern Baja California, southern, and central California.*

	Group	Sub-group	Number of food type entries in a sub-group	Incidence	
				Number	Percent to total
Zooplankton	Crustaceans	Copepods[1]	10	1198	29.32
Zooplankton	Crustaceans	Euphausiids[1]	5	390	9.54
Zooplankton	Crustaceans	Others[1]	24	487	11.92
			39	2075	50.78
Zooplankton	Other zooplankters	Pelagic worms	9	333	8.15
Zooplankton	Other zooplankters	Thaliaceans	4	272	6.66
Zooplankton	Other zooplankters	Appendicularians	2	152	3.72
Zooplankton	Other zooplankters	Molluscs	6	144	3.52
Zooplankton	Other zooplankters	Bryozoan "cyphonautes"	1	111	2.72
Zooplankton	Other zooplankters	Fish eggs and larvae[2]	7	104	2.55
Zooplankton	Other zooplankters	Other miscellaneous	14	175	4.28
Zooplankton	Other zooplankters	Indeterminate soft parts and remains	3	170	4.16
			46	1461	35.76
Total			85	3536	86.54
Phytoplankton	Diatoms	Diatoms	1	295	7.22
Phytoplankton	Other phytoplankters	–	3	154	3.77
Total			4	449	10.99
Foreign matter	–	–	7	101	2.47
Grand total			96	4086	100.00

[1] All stages and remains.
[2] Included anchovy eggs and larvae.

importance as food items are caladocerans (*Podon polyphemoides* and *Evadne nordmanni*).[13] Larvae of decapods and bivalves were found in quantities of "slight significance in respect to total food supply." The same was true of the eggs of various marine organisms. Most of the fish eggs in the stomach contents were eggs of anchovy and of *Prionotus* species.[14]

Among the phytoplankters found in the stomach contents, species of the diatoms *Coscinodiscus* and *Triceratium*, and of the dinoflagellate *Exuviaella* were the plant organisms most frequently encountered. De Ciechomski observes that "although these organisms are found in many individuals and are occasionally

[13] The great quantities of cladocerans in the intestinal contents, especially during some winter and summer months, coincided with the abundance of these microcrustaceans in the plankton.
[14] Presence of fish eggs in the stomachs, especially during the spring and summer, coincided with the appearance of these eggs in the plankton.

FIGURE 8. Not the stars in the sky! This is a mass concentration of juvenile northern anchovy (*Engraulis mordax*) feeding on the microplankton consisting mainly of microcalanids, their eggs and nauplii, with insignificant admixture of bryozoan "cyphonautes" larvae, and occasional diatoms (*Coscinodiscus* species), as uncovered by examination of the fish stomach contents.

With gill covers stretched wide they filtered water when raising to the surface in vertical wave pattern. The sun reflection from the gill covers and fish sides is seen in the picture. Reaching close to the surface, the fish shut their mouths, and submerge for about 7–10 feet, and then repeat the sequence.

San Jose Point, Baja California, Mexico, close to the shore line; early morning hour, September 26, 1965. Specimens in the collection numbered 39–50.

Size range of the fish in this school was within 67–91 mm. (standard length).

very abundant, their significance in the total weight is low. During the summer a lesser contribution of the phytoplankton organisms is observed in the anchovy diet."

Among other things, de Ciechomski mentioned that in juveniles 41–90 mm. long she found amounts of detritus and very fine sand grains with great quantity of *Triceratium*, a diatom abundant in water layers close to the bottom. In the spring the skeletons of benthic foraminiferans were found in the food of the individuals.[15] In closing, de Ciechomski identified the Argentine anchovy as a

[15] This, as in case with our northern anchovy, exposes behavioral tendency to descend to near-bottom horizon in bright sunshine.

zooplanktophagous animal in comparison with the phytoplanktophagous Peruvian anchoveta, *Engraulis ringens*, and concludes that "all of the information obtained suggests that the larvae and juveniles of the [Argentine] anchovy do not select much of their food, and that they feed upon the food which is present in greater abundance.[16] As a consequence, their diet may be quite dependent upon the patterns of plankton dispersal. Another very important factor is the accessibility of the food as determined by the size of the prey and dimensions of the mouth of the fish."

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CONCLUSIONS

On the basis of the materials analyzed and visual observations incorporated in the present report, and referring to the literature cited, the following summarized conclusions can be reached:

(1) The northern anchovy, *Engraulis mordax* Girard, is a planktophagous species.
(2) It is an omnivorous animal living either on phytoplanktonic or zooplanktonic organisms, or on both at the same time.
(3) Zooplankters seem to be preferred in the anchovy diet.
(4) Among zooplankters, crustaceans in all stages, from egg to adult form, appear to be the most dominant food objects found in the stomach contents.
(5) Of crustaceans, the copepods and euphausiids are most frequently and abundantly found in the stomachs, and they appear to be the most important food items in the diet of the northern anchovy, as well as in the diet of other anchovies whose food habits were already reported by other investigators.
(6) Though phytoplanktonic organisms were also found in the stomachs (sometimes they constituted a dominating item, or they even contributed up to

[16] All 30 food objects listed by de Ciechomski for the larval and juvenile Argentine anchovy are also present on the menu of the northern anchovy.

100 percent of the contents), their role in the anchovy diet seems on the whole negligible.

(7) In mode of feeding, the northern anchovy is primarily a filter feeder, but may also be a particulate or selective feeder, depending on the size of the available food.

(8) In relation to feeding habits, the northern anchovy is a diurnal animal, feeding mostly during the day.

(9) From the larval stages through adult life, the northern anchovy shows an apparent preference for the second link in the food chain. This is in contrast to the food of the Peruvian anchoveta, *Engraulis ringens,* which is reported to be chiefly phytoplankton.

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APPENDIX A.

A list of partially identified copepods from the stomachs of the Northern anchovy—*Engraulis mordax* (Girard). Identified by Professor Martin W. Johnson

1. *Acartia* spp.
2. *Calanus helgolandica*
3. *Calanus* spp.
4. *Candacia* sp.
5. *Centropages* sp.
6. *Corycaeus* sp.
7. Cyclopoid copepods
8. *Eutherpina* sp.
9. Herpacticoid copepods
10. *Labidocera trispinosa*
11. *Metridia* sp.
12. *Microcalanus* spp.
13. *Microsetella* sp.
14. *Oithona* sp.
15. *Onacea* sp.
16. *Paracalanus* spp.
17. *Pseudocalanus* spp.
18. *Rhyncalanus* sp.
19. *Temora* sp.
20. Calanoid copepods

APPENDIX B.

A list of diatoms and dinoflagellates found in the stomach contents of northern anchovy (*Engraulis mordax*) collected in Baja California and southern and central California waters in 1965–1968. Identifications were made chiefly by Dr. G Dallas Hanna, California Academy of Sciences.

DIATOMS

1. *Bacteriastrum* sp.
2. *Biddulphia longicruris*
3. *Chaetoceros decipiens*
4. *Chaetoceros* sp.
5. *Coscinodiscus asteromphalus*
6. *Coscinodiscus excentricus*
7. *Coscinodiscus oculis-iridis*
8. *Coscinodiscus radiatus*
9. *Coscinodiscus stellaris*
10. *Coscinodiscus wailesii*
11. *Coscinodiscus* sp.
12. *Dicladia capreolus*
13. *Diploneis smithii*
14. *Distephanus speculum*
15. *Eucampia* sp.
16. *Lithodesmium* sp.
17. *Navicula distans*
18. *Nitzschia* sp.
19. *Pleurosigma* sp.
20. *Rhizosolenia hebatica*
21. *Rhizosolenia* sp.
22. *Skeletonema costatum*
23. *Skeletonema* sp.
24. *Stephanopyxis turris*
25. *Thalassiosira* sp.
26. *Thalassiothrix* sp.

DINOFLAGELLATES

1. *Ceratium furca*
2. *Ceratium longipes*
3. *Ceratium macroceros*
4. *Ceratium tripos*
5. *Ceratium* sp.
6. *Dinophysis* sp.
7. *Peridinium* spp.

APPENDIX C.

SAMPLE LXIV.

On September 21, 1965, at 10:15 P.M. in San Quintin Bay, Baja California, Mexico, 2.8 miles offshore, 200 Pacific sardines and 10 anchovies were captured using electric light as attractant and a blanket net as collecting gear. Depth of water was 17 fathoms. Stomachs of 11 sardines 203–235 mm. standard length and 10 stomachs of anchovy 105–117 mm. standard length were preserved. Records of examination of the contents of stomachs are given below.

Northern anchovy *Engraulis mordax* Nos. 395–404	Pacific sardine *Sardinops caerulea* Nos. 405–414 and 414a
All stomachs were filled to capacity	Three stomachs were filled to full capacity ("gorged"); two—¾ capacity; two—half-filled; and four—poor.
In all stomachs large copepods constituted dominating food item (up to 98%). Among these copepods other zooplankters were scattered in insignificant numbers, such as small copepods, decapod larvae, amphipods, oikopleura, etc. No diatoms were found.	In all stomachs, even with poor filling, large copepods were dominating food item (up to 98–99%). Among these copepods there were a few other zooplankters present either by single individuals or in small numbers. To this category belonged small copepods, brachyuran zoea and megalopa, isopods, amphipods, euphausiid larvae, copepod eggs, copepod fleshy parts, chunks of polychaete worms, salps, hemicordate larvae, oikopleura. Small copepods and copepod eggs were more numerous than the rest of the other zooplankters. No diatoms were present. In one stomach a fragment of algae (kelp-like type) was found. Foreign matter, such as many fine mica flakes and a few fine sand grains, was found in stomach No. 413.
Similarity in food items is evident.	

APPENDIX D.

Frequency of occurrence of various food items in the stomach contents of 12 jack mackerel, *Trachurus symmetricus* (Ayres) 87–102 mm. standard length from the catch of 3,000 fish, using electric light and blanket net, on September 21, 1965, at 10:15 P.M. in San Quintin Bay, Baja California. Seven stomachs were filled to full capacity, 2 to ¾ capacity, and 3 stomachs to ½ capacity.

Description	*Position*			*Total*
	Dominating	*Second Place*	*Insignificant*	
Copepods, large[1]	7	4	1	12
Euphausiids, adult	3	1	1	5
Mysids	1	–	4	5
Indeterminate fleshy material	1	3	1	5
Crustacean fleshy parts	–	–	5	5
Oikopleura	–	1	3	4
Brachyuran zoea	–	–	10	10
Hemicordata larvae	–	–	10	10
Jellyfish larvae and parts	–	–	6	6
Chaetognaths	–	–	6	6
Copepod eggs	–	–	6	6
Fine sand grains (foreign matter)	–	–	6	6
Microcalanids	–	–	4	4
Algae (kelp-like fragments)	–	–	4	4
Foraminiferans (bottom living)	–	–	4	4
Minute pebbles (foreign matter)	–	–	4	4
Isopods	–	–	3	3
Salps	–	–	3	3
Brachyopod larvae	–	–	3	3
Fine mica flakes (foreign matter)	–	–	3	3
Eggs (?)	–	–	3	3
Larvae (?)	–	–	2	2
Medusae	–	–	2	2
Small copepods	–	–	2	2
Nemertean worm larvae (pelagic)	–	–	2	2
Pteropods (*Limacina* sp.)	–	–	2	2
Cephalocordata larvae	–	–	2	2
Sagitta (worms)	–	–	2	2
Porcellanid crab larvae	–	–	1	1
Balanus "cypris" larvae	–	–	1	1
Polychaete worms	–	–	1	1
Polychaete worm eggs	–	–	1	1
Gastropod larvae	–	–	1	1
Amphipods	–	–	1	1
Shrimp, small	–	–	1	1
Mantis shrimp larvae	–	–	1	1
Cumaceans	–	–	1	1
Euphausiid calyptopis	–	–	1	1

[1] Includes adult copepods, their fleshy parts and remains (carapaces).

APPENDIX D. (*Continued*)

Description	Position			
	Dominating	Second Place	Insignificant	Total
Foraminiferans (pelagic)	–	–	1	1
Fish eggs	–	–	1	1
Fish eggs with larva inside	–	–	1	1
Diatoms	–	–	1	1
Fish scales (foreign matter)	–	–	1	1
Rough sand grains (foreign matter)	–	–	1	1
TOTAL	12	6	121	142

APPENDIX E.

SAMPLE LVIII. October 18, 1966, 8:13 P.M.; 14 mi. E. × N. Point Conception, southern California, 4 m. offshore; 17 anchovies 107–131 mm. standard length and 2 hakes 129–132 mm. standard length caught by midwater trawl net. Stomach contents of 7 anchovies and 2 hakes examined.

Dominating food items

Anchovy (*Engraulis mordax*)		Hake (*Merluccius productus*)	
No. 783 Euphausiids		No. 790 Euphausiids	
No. 784 Copepods		No. 791 Euphausiids	
No. 785 Euphausiids			
No. 786 Salps			
No. 787 Polychaete worms			
No. 788 Euphausiids			
No. 789 Empty			
Euphausiids	50%	Euphausiids	100%
Other	50%		
TOTAL	100%	TOTAL	100%